

ALPOVA, A NEW GENUS OF RHIZOPOGONACEAE,
WITH FURTHER NOTES ON LEUCOGASTER AND
ARCANGELIELLA

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In the summer of 1930, Dr. Alfred H. Povah, of the Isle Royale Lake Superior Survey, made several collections of a very puzzling member of the Hymenogasteraceae (*sensu latiore*). This fungus, which has been referred to a new genus, is very curious in uniting the peridial characters of *Hysterangium* with the gleba of *Leucogaster*, the scattered basidia of *Melanogaster*, and the spores of *Rhizopogon*. This genus should be placed in the Rhizopogonaceae of the author.¹

Before discussing the morphology of *Alpova* in detail it might be of interest to turn our attention to the main evolutionary tendencies which have been at work in the Gasteromycetes, a seemingly highly specialized group which has developed quite independently of the Hymenomycetes, although it must be admitted that some members bear a striking resemblance to the Agaricaceae. The writer prefers to regard this as a convergence phenomenon connected with spore dispersal rather than of phylogenetic significance. If one considers the gasteromycetous condition of certain Boletaceae, one is tempted to consider the Gasteromycetes the more primitive group and that perhaps the Agaricales have developed from them.

As a working hypothesis, it seems probable that the following statements are true:

1. The primitive Gasteromycetes consisted of spherical or somewhat irregular fructifications with no differentiated sterile tissues and no stipe, the rhizomorphs on which the fruit-bodies were borne ending at the peridium. Gradually a cushion was formed at the point of attachment from which the larger tramal plates originated. This increased in size, penetrating farther into

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¹Dodge, C. W. Gasteromycetes in Gäumann & Dodge, Comparative morphology of fungi, pp. 468-470. New York, 1928.

the fructification until it fused with the peridium at its tip, forming a percurrent columella. Along with this development, the end of the rhizomorph developed a stipe to raise the fertile portion of the fructification above the substrate for better dispersal of spores.

2. The primitive peridium consisted of a single layer of hyphal tissue rather loosely woven. The additional layers have been developed in connection with more highly specialized fructifications in response to a more rigorous environment or to secure more efficient dispersal of spores.

3. The primitive gleba consisted of a loose, indefinite tramal tissue in which conidia, as well as the basidia, were borne. As the conidia lost their main function and degenerated *in situ*, they formed a gel which nourished the developing basidium and spores. In time they disappeared and left cavities in the gleba at approximately the same time that the basidia became organized in hymenia.

4. The primitive basidium was an eight-spored stichobasidium which gradually shortened its axis and became a chiasmobasidium, reducing its spore number in many groups to four and in a few species to one.

5. The primitive spore was smooth, generally ellipsoidal and hyaline, and symmetrically placed at the tip of the sterigma. Spore discharge was at first effected by the degeneration of the basidium or the rupture of the sterigma, perhaps by increasing pressure in the basidium. In many of the more primitive Gasteromycetes, portions of the broken sterigmata may still be seen attached to the spore. The hymenomycetous type has progressed still farther with a highly developed mechanism for the discharge of an asymmetrically placed spore, so accurately described by Buller.² This hymenomycetous type is so fixed that it persists even in the gasteromycetous condition of *Boletinus decipiens* (Berk. & Curtis) Peck, where nearly all the other hymenomycetous characters have completely disappeared.

While the foregoing statements seem to be true, one sometimes finds an obviously highly developed form which has retained some primitive character, e. g., the basidium and spores of the Phal-

² Buller, A. H. R. *Researches in fungi* 3: 1-496. 1924.

laceae remain comparatively primitive whereas the tissues of the fructification have been highly specialized, even to the extent of securing insect dispersal of the spores.

When we turn our attention to *Alpova* in the light of the foregoing discussion, we find a very primitive member of the Rhizogonaceae. The peridium is pseudoparenchymatous, of large, thin-walled cells, a character which our working hypothesis considers rather advanced, especially since it is comparatively rare elsewhere in the family. The trama, too, is composed of large, thin-walled, parallel hyphae, giving it a pseudoparenchymatous appearance. However, we have no highly differentiated sterile tissues.

The basidia are irregularly distributed through the fertile tissue between the layers of trama, apparently rising from large thin-walled hyphae from the trama which penetrate the gel formed by the decaying conidia (?). In *Leucogaster* we have a similar gel, but the basidia, although long-pedicellate, are always developed directly from the trama and form a loose hymenium. On the other hand, in the highly developed Podaxaceae, in both *Phellorinia* and *Podaxis* we have the basidia borne in compact clusters from small funiculi of large thin-walled hyphae (see pl. 40, fig. 6, for appearance of *Podaxis Farlowii*³).

The curious structures which form the gel into which the basidia grow are still unexplained. E. Fischer⁴ considered them large sterile cells formed in the ground tissue as a kind of pseudoparenchyma in an early stage of *Leucogaster floccosus* Hesse, whereas the writer,⁵ in view of the curious way in which they are borne, considered them to be vestigial conidia which may have lost their original function. Plate 40, fig. 4, shows a somewhat similar organ in an otherwise degenerated "cavity" of *Alpova*. Whether the much larger hyaline spheres also found in the fertile tissues of *Alpova* are borne in this manner is uncertain, since I have not been able to find their points of attachment.

³ I am deeply indebted to Miss Elizabeth Morse of the University of California for excellent material of both *P. Farlowii* Masee, from which these figures were made, and of *P. anomalus* Lloyd, which shows the same condition.

⁴ Fischer, E. Mykologische Beiträge, 25. Jugendstadien des Fruchtkörpers von *Leucogaster*. Naturf. Ges. Bern, Mitt. 1921: 301-307 [20-26]. 1922.

⁵ Zeller, S. M. & C. W. Dodge. *Leucogaster* and *Leucophlebs* in North America. Ann. Mo. Bot. Gard. 11: 390-391. 1924.

The basidium of *Alpova* is especially interesting in that it is always eight-spored, which would point to a very primitive condition if we accept the hypothesis that the basidium and the ascus have been derived from a common ancestor after the number of ascospores in the ascus had been fixed at eight.⁶ Eight spores per basidium is a very rare phenomenon in the Basidiomycetes, and I know of very few species where the number seems so fixed as in *Alpova*. In the Gasteromycetes, however, there are many species with basidia bearing more than four spores, as well as several species where occasionally or regularly only one very large spore is borne. In species where the number of spores has been fixed at four, many cases have been reported where the spore nucleus divides promptly, producing a binucleate spore. Hence it appears that meiosis immediately followed by a vegetative division giving eight nuclei is still fixed in the Gasteromycetes, although it is very rare in the Hymenomycetes.

The basidium of *Alpova* is long and slender, apparently of the stichobasidial type, although I have not had the opportunity to observe nuclear divisions in it. This type is apparently very rare in the Gasteromycetes, occurring only in a few American species of *Leucogaster*, whereas the other species of that genus appear to be of the chiasmobasidial type. The occurrence of basidia on long, slender funiculi which traverse the fertile region is suggestive of conditions found in the Podaxaceae. In the latter, however, the basidium has already become four-spored with a thick-walled, colored spore, has shortened its long axis as a chiasmobasidium (see pl. 40, fig. 7, *Podaxis Farlowii*), and assembled in dense tufts about nodes of the funiculi, whereas in *Alpova* the basidia are borne singly along the funiculi.

The spores of *Alpova* are ellipsoidal with a slightly thickened, smooth wall, hyaline under the microscope but colored brownish in mass, very much like *Rhizopogon* but much smaller in our species. This tiny ellipsoidal to bacilliform spore has been retained by several genera of lower Gasteromycetes and by the highly specialized Nidulariaceae, Phallaceae, and Clathraceae.

⁶ Gäumann, E. A. Vergleichende Morphologie der Pilze. pp. 399-401. Jena, 1926.

ALPOVA gen. nov.

Fructificationes sphaericae, sine columella, sine stipite; gleba gelatinosa, locelli impleti, basidia in funiculis per locellos vagantibus, octospora; sporae ellipsoideae.

Alpova cinnamomeus Dodge, sp. nov. Pl. 40, figs. 1-5.

Fructificationes sphaericae, 5-20 mm. diametro metientes, cinnamomeae; peridium 300 μ crassitudine, cellulis magnis pseudo parenchymate; gleba cinnamomea, gelatinosa; locelli cellulis magnis qui in gelatina dilabunt, impleti; septa tenuia, 25-50 μ crassitudine pseudoparenchymate vel hyphis magnis parallelis qui pseudoparenchymatem simulant; basidia in funiculis hypharum magnarum per locellos vagantibus, longissima, 20 x 22 x 4-5 μ , octospora, sterigmatibus curtis; sporae hyalinae sub lente, cinnamomeae acervatae, ellipsoideae, 3-4 x 1.5-2.5 μ .

Type: Tobin Harbor trail, Isle Royale, Michigan, *C. A. Brown Fp. 73*, in Herb. Univ. Michigan.

Fructifications spherical, 5-20 mm. in diameter, pinkish buff to cinnamon buff, turning hazel to auburn (Ridgway); peridium thick, 300 μ , composed of large-celled pseudoparenchyma; gleba clay-color, turning Hessian brown, gelatinous, the spaces between the septa at first filled with large spherical cells (conidia?) which finally disintegrate; septa of large, thin-walled, hyaline, parallel hyphae which simulate pseudoparenchyma; basidia on slender funiculi as in the Podaxaceae, scattered irregularly in the gel, very long and slender, 20-22 x 4-5 μ , eight-spored with sterigmata about 1 μ long; spores hyaline under the microscope, pale brown in mass, ellipsoidal, 3-4 x 1.5-2.5 μ .

Half buried in soil, often under *Alnus*, Isle Royale, Lake Superior, July to September.

In view of the frequent affinities which plants of this region show with those of the Pacific slope, it is interesting to note that the species of *Leucogaster* to which this species appears most closely related are all Californian.

Specimens examined:

Michigan: Isle Royale, Tobin Harbor, *C. A. Brown Fp. 28, 73* type; Rock Harbor Trail, *A. H. Povah & G. L. Lowe Fp. 92*, *C. A. Brown Fp. 298*; Siskowet Outlet at Siskowet Bay, *A. H. Povah Fp. 635* (in Herb. Univ. Michigan).

During a recent visit to the herbaria of Europe the writer was able to study the types of most of the species of the Hymenogasteraceae. The following notes on synonymy of *Leucogaster* may

be of interest in this connection, since the genus seems so closely allied to *Alpova*.

Leucogaster nudus (Hazslinszky) Hollós, Mus. Nat. Hungarici Ann. 6: 319. 1908; Magyarország Földalatti Gombai, 98, 208. 1911 (excl. syn.).

Hydnangium nudum Hazslinszky, K. K. Zool.-bot. Ges. Wien, Verhandl. 25: 64-65. 1875; Magyar Tudományos Akad. Természettud. Közl. 13: (9). 1875 [often cited as Magyarhon hasgombai, 9. 1876]; Hedwigia 16: 44. 1877; Saccardo, Syll. Fung. 11: 172. 1895.

Hydnangium virescens Quélet, Soc. d'Émul. Montbéliard Mem. 1875 [Champ. Jura et des Vosges 3: 110. 1875]; Enchiridion, 248. 1886; DeToni in Sacc. Syll. Fung. 7: 177. 1888.

Leucogaster luteomaculatus Zeller & Dodge, Ann. Mo. Bot. Gard. 11: 394-395. 1924.

Type: cotype in Berlin. Authentic material of *Hydnangium virescens* collected at Waiter in the Vosges by Solms-Laubach and determined by Quélet in Upsala Bot. Mus. Inquiry in France failed to locate Quélet's herbarium if he left one. However, there is much material and many paintings in the Elias Fries Herbarium in Upsala. Apparently the situation is much the same here as in the case of Elias Fries' Swedish species, which are much more fully represented in the M. J. Berkeley Herbarium at Kew than they are in his own herbarium at Upsala. Type of *Leucogaster luteomaculatus* in the Farlow Herbarium at Harvard University.

L. citrinus (Harkness) Zeller & Dodge.

This species has also been seen from Mt. Lofty, South Australia, *J. B. Cleland* 4, not previously known outside California.

A study of all the types involved shows that the following species of *Octaviania* and *Hydnangium* should be transferred to *Arcangeliella*. The group of species centering about *Arcangeliella Stephensii* is separable with difficulty, and it is quite possible that they should be considered only varieties.

Arcangeliella rosea (Harkness) Zeller & Dodge, n. comb.

Octaviania rosea Harkness, Cal. Acad. Sci. Bull. 1: 29. 1884.

Type: in Dudley Herb. at Leland Stanford Jr. University.

A. Stephensii (Berk. & Br.) Zeller & Dodge, n. comb.

Hydnangium Stephensii Berk. & Br. Ann. & Mag. Nat. Hist. I. 13: 352. 1844.—*Octaviania Stephensii* Tulasne, Fung. Hypog. 78. 1851.—*Octavianina Stephensii* O. Kuntze, Rev. Gen. Pl. 3²: 501. 1898.

Type: in Kew, British Museum, and in Museum d'Histoire Naturelle de Paris.

A. Ravenelii (Berk. & Curtis) Dodge, n. comb.

Octaviania Stephensii v. *Ravenelii* Berk & Curtis in Tulasne, Fung. Hypog. xvii. 1851.—*Hydnangium Stephensii* v. *Ravenelii* Berk. Grev. 2: 33. 1873.—*Hydnangium Ravenelii* Berk. & Curtis in Curtis, Bot. N. Car. 110. 1867.—*Octaviania Ravenelii* Lloyd, Myc. Notes 67: 1140. 1922.

Type: in Kew, in British Museum, and at Farlow Herbarium.

A. australiensis (Berk. & Br.) Dodge, n. comb.

Hydnangium australiense Berk. & Br. Linn. Soc. London, Trans. II. Bot. 2: 66. 1883.—*Octaviania australiensis* Cooke, Handbook Austral. Fungi, 246. 1892.—*Hydnangium brisbanense* Berk. & Br. in Cooke, Handbook Austral. Fungi, 247. 1892.—*H. glabrum* Rodway, Papers & Proc. Roy. Soc. Tasmania 1920: 157. 1921.

Type: both *H. australiense* and *H. brisbanense* were based on the same specimen, Brisbane, *F. M. Bailey* 188, at Kew and in British Museum. Cotype of *H. glabrum* in Dodge Herb.

EXPLANATION OF PLATE

PLATE 40

Figs. 1-5. *Alpova cinnamomeus* Dodge.

Fig. 1. Section of peridium, $\times 285$.

Fig. 2. Section of fructification showing peridium and gleba. The white areas of the gleba represent the hyaline septa. $\times 38$.

Figs. 3, 5. Basidia showing both top and side views. $\times 766$.

Fig. 4. Hypha bearing the large thin-walled cells (conidia?) which gelify before the basidia develop. $\times 766$.

Figs. 6, 7. *Podaxis Farlowii* Masee.

Fig. 6. Funiculi showing verticillate tufts of basidia. $\times 100, 433$.

Fig. 7. Basidia and basidiospores. $\times 1400$.